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THE ELECTROPHYSIOLOGY OF THE ORGAN-PIPE CORAL, *TUBIPORA MUSICA*

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Although corals constitute remarkable examples of colonial organization, their behavior has received little attention since Horridge studied the effects of mechanical and electrical stimulation on a variety of corals (Horridge, 1956, 1957). He found two separate yet sometimes interacting levels of behavior: that of the individual polyps and that of the colony as a whole, with the latter involving coordinated activities of two or more polyps.

Individual polyps were found to feed, withdraw and perform other activities without affecting the remainder of the colony. However, with appropriate stimulation, this autonomy broke down and colonial responses involving retraction of large numbers of polyps were evoked. Such colonial responses spread in one of two ways. Certain corals, typified by *Tubipora*, responded in a through-conducting manner, with each wave of activity affecting all parts of the colony. In other corals, the spread was incremental, each stimulus serving to increase the size of the responding area (Horridge, 1957).

Apart from the question of how incremental spread can occur in a conduction system composed of all-or-nothing conducting units, such behavior poses two problems. First, how can the behavior of individual polyps be kept separate from those of the remainder of the colony; and second, how can that autonomy be broken down so as to produce a colonial response?

In the pennatulid *Renilla köllikeri*, the autonomy of individual polyps is maintained by the necessity for a complex and not fully understood interaction between two conduction systems within the colony (Anderson and Case, 1975). One conduction system, the Zooid Nerve Net (ZNN) is restricted to individual polyps where it is responsible for polyp withdrawal. The ZNN can be activated by a through-conducting colonial nerve net. While colonial nerve net activity can simultaneously activate the ZNN in all the polyps, there is a degree of flexibility inherent

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in the interaction that allows each autozooid to retain a measure of control over whether or not it withdraws during colonial nerve net activity.

Through-conducting nerve net activity has been recorded from a variety of alcyonarians (Shelton, 1975c; Anderson and Case, 1975) and more recently from certain madreporian hard corals (Shelton, 1975a, d). Furthermore, there is good evidence that there are two colonial conduction systems in certain pennatulids (Shelton, 1975c; Anderson and Case, 1975) and perhaps some hard corals (Shelton, 1975d). However, with the exception of *Renilla,* no colonial anthozoans have been studied from the viewpoint of how the autonomy of the individual polyps is maintained.

Horridge's descriptions of the behavior of *Tubipora* (Horridge, 1957) indicate differences between it and *Renilla* in the mechanisms by which colonial activity affects the polyps. In *Renilla* there are varying requirements for the interaction between the colonial conduction system responsible for colonial polyp withdrawal and the conduction system in each polyp. Different polyps respond to different numbers of colonial pulses. The result is that colonial polyp retraction is spatially irregular; widely separated polyps may contract nearly synchronously, while there may be major delays between the onset of contraction in neighboring polyps. In *Tubipora,* polyps withdraw in sequence so as to produce a wave of twitching and withdrawal that spreads across the colony away from the point of stimulation.

This rather large difference in the behavior of the two colonies suggests that the mechanisms by which the autonomy of the polyps in *Tubipora* colonies is maintained may differ from that described for *Renilla.* Consequently, this problem was given special attention during this study which comprised part of a series of investigations of conduction systems in colonial anthozoans.

Materials and Methods

Specimens of *Tubipora musica* Linnaeus (sub-class Alcyonaria, order Stolonifera) were collected from the reefs surrounding the Banda Islands, Indonesia. Large populations of the coral were found only in a few sheltered, shallow locations. Large colonies, frequently measuring up to three feet in diameter were observed underwater, while more detailed studies were conducted on 8–12 cm diameter colonies maintained in aquaria. At all stages of the collections and experiments, great care was taken to ensure that the colonies were never removed from the water. When colonies were exposed to air, bubbles became trapped between the pipes that comprise the colony and remained there upon submersion. This resulted in rapid decay of the colony. The water in the aquaria was changed regularly and filtered continually. The colonies were not fed. It did not prove necessary to control the temperature of the water in the aquaria since it maintained itself at approximately 28° C, the temperature of the surface water in the region. Electrical recordings were made with suction electrodes in the manner described previously (Anderson and Case, 1975).

Results

Tubipora musica colonies are composed of parallel arrays of pipes or tubes linked together at regular intervals along their length by connecting platforms

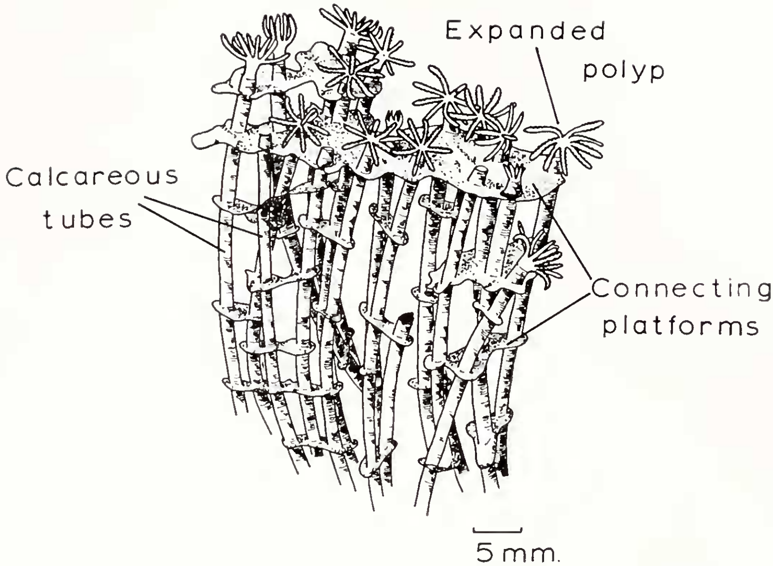

FIGURE 1. Diagram of a small portion of a *Tubipora musica* colony.

(Fig. 1). The skeletons are a dull red color but the living colonies usually appear various pale shades of green, blue or purple due to the color of the expanded polyps. Generally any one colony is composed of polyps of a single color, although occasionally portions of large colonies were found to be composed of polyps of a different color from that of the remainder of the colony. In many of these cases, there is a distinct boundary between the two color regions. If one part of such a coral was stimulated, the resulting wave of withdrawal would pass across the boundary, indicating that these specimens were functionally single colonies.

Since the behavior of *Tubipora* has been well described by Horridge (1957) only a summary is given here with a few additional observations. When a tentacle of a polyp was lightly touched with a probe, it, and the neighboring tentacles of the polyp, shortened and bent away from the oral disk. Only rarely would a tentacle bend toward the oral disk in the manner described by Horridge. If the same tentacle were touched again, all the remaining tentacles shortened and bent away from the mouth; and a third such stimulus caused polyp withdrawal. During withdrawal the tentacles were elevated and the polyp pulled down into its tube in discrete twitches. Withdrawal of one polyp usually had no effect on the remainder of the colony. If stimuli of higher intensities than those required to evoke responses from individual polyps were used, a colonial response was invariably produced. In *Tubipora* there appeared to be only one colonial response; polyp retraction. A mechanical stimulus evoked a wave of polyp retraction which spread across the colony away from the point of stimulation. It proved very difficult to control the intensity of the mechanical stimuli to the degree that only one wave of polyp retraction was produced, and frequently, several successive waves of twitch-

ing followed each stimulus. During the colonial response, the withdrawal behavior of the polyps appeared almost identical to that described above for withdrawal of polyps stimulated individually. That is, the first wave of colonial activity involved a shortening and a downward movement of the tentacles of the polyps, while the second wave consisted of an upward flexion of the tentacles prior to actual retraction of the polyp, an action which was completed in discrete stages during the succeeding waves of colonial activity.

Similar colonial responses could be evoked with electrical stimulation. A single supra-threshold stimulus did not produce retraction but apparently activated the colonial conduction system, as evidenced by scattered tentacle waving of polyps across the colony. A second stimulus produced a single twitch from all the polyps and as described above, this involved shortening and depression of the tentacles. Successive stimuli evoked further waves of activity with each of the above-mentioned stages in the retraction response comprising the activity associated with each wave. The size of the twitches or movements associated with each stage of the response was greater at shorter interstimulus intervals.

Electrical activity associated with this behavior was recorded with suction electrodes attached to the colony. While potentials could be recorded from all parts of the polyps, clear, long-term records could only be obtained from the oral disk. Electrical stimuli were applied through an additional suction electrode, frequently attached to a polyp in a part of the colony displaced from the recording sites. Each

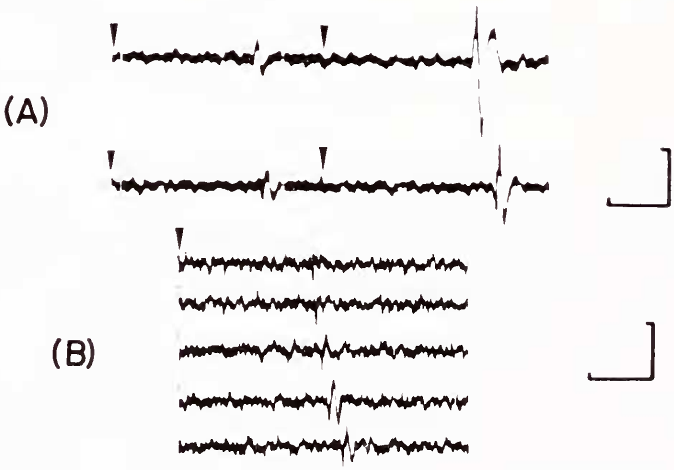

FIGURE 2. (A) Electrical activity recorded from *Tubipora* through two suction electrodes attached to different polyps. Each of two electrical stimuli (marked with a dark triangle) evokes a single through-conducted potential. While the potential evoked by the first stimulus consists of a single unit, the potential evoked by the second stimulus contains an additional component interpreted as a muscle action potential. (B) Facilitating potentials recorded through a single electrode. Five stimuli were applied at two second intervals. The first stimulus gives rise to a single small potential that reappears after all subsequent stimuli. Later stimuli evoke potentials composed of an additional facilitating muscle action potential. The ordinate is 10 μV, abscissa, 200 msec.

electrical stimulus evoked a single through-conducted potential (Fig. 2A). The potential evoked by a single stimulus or the first of a series was a simple, invariant, small amplitude (5 μV), short duration (20 msec) impulse that was never associated with any colonial activity other than the scattered tentacle waving mentioned above. Subsequent stimuli evoked more complex potentials composed of two parts: an initial component identical to that evoked by the first stimulus of the series, and a second, slower and larger component. Both the amplitude and the duration of the second component varied with the interstimulus interval, being greatest at shorter intervals. [Compare Fig. 2A (interstimulus interval approximately 650 msec) with Fig. 2B (interstimulus interval, 2000 msec).] During a series of pulses, the amplitude and duration of the second component increased and later decreased, the size at any one time being a function of stimulus frequency and pulse number. The presence of the two components is apparent in most but not all records.

Occasionally, the second component would be recorded after a single stimulus. Whenever this happened, however, there was a distinct colonial response, beyond the simple tentacle waving normally associated with a single stimulus. Since the second component was always found to be associated with polyp retraction, it was interpreted as being a muscle action potential associated with activation of those muscles involved in polyp retraction. As the interval between a pair of stimuli was increased, the amplitude of the muscle action potential evoked by the second shock declined. In some trials, clear muscle action potentials followed shocks separated by as much as ten seconds, but the neuromuscular facilitatory period was quite variable and often considerably shorter than ten seconds. In behavioral experiments in which the interval between two stimuli was increased until the second had no apparent effect, Horridge (1957) found that the facilitatory period for *Tubipora* was about four seconds.

Mechanical stimuli strong enough to evoke a colonial response evoked potentials identical to those that follow electrical shocks. Each mechanical stimulus usually evoked a single potential. While two potentials sometimes followed a single mechanical stimulus, bursts of more than two were never recorded. When mechanical stimuli of the strength necessary to produce multiple waves of twitching were used, all records subsequent to the application of the stimulus were obscured by a movement artifact. Horridge (1957) found that a strong mechanical stimulus gave rise to successive waves of twitching which spread across the colony at a rate of 2/second. In this study the mean inter-pulse interval for the paired potentials recorded after some mechanical stimuli was 541 msec, a figure that corresponds well with that found by Horridge (1957).

The conduction velocity of the through-conducted potentials was determined from the difference in the response latency between two recording sites. The conduction velocity was greatest for the first potential in a series (mean value 18 cm/sec at 28° C) and diminished for subsequent potentials. The final value of the conduction velocity during repetitive stimulation depended on the frequency and number of stimuli. For example, in one trial, the conduction velocity fell from 18 cm/sec after the first stimulus to 12 cm/sec after the fifth stimulus of a series applied at one per second. The relative refractory period was 250 msec.

Potentials similar in shape to those evoked by stimulation were recorded spontaneously at a rate of approximately one to two every minute. Some of these were through-conducted, appearing almost simultaneously on the records from widely separated polyps. Others were not through-conducted, but appeared only on records from a single polyp. For clarity, the former class of spontaneous potentials will be referred to as the spontaneous through-conducted potentials, and the latter as the isolated potentials. Neither type of spontaneous potential appeared to be recorded in any obvious pattern, and there were no apparent interactions between them.

Isolated potentials were restricted to the polyp in which they originated. If two electrodes were attached to adjacent polyps, spontaneous isolated potentials were still recorded, indicating that these potentials were not propagated between neighbors. In further tests to verify that there was indeed no propagation of isolated potentials out of individual polyps, two recording electrodes were attached to widely separate polyps. The polyps surrounding one of those bearing an electrode were then lightly touched and made to retract. In almost every case, the stimulated polyps could be made to retract completely without potentials being recorded by the electrode on the adjacent polyp. In the few cases when a potential was recorded from the adjacent polyp the simultaneous appearance of a similar potential on the record from the more distant electrode revealed that the recorded potential was a result of activation of the colonial conduction system. If the polyp to which an electrode was attached were touched lightly until a tentacle shortened or bent down from the oral disk, an isolated potential was recorded.

To test whether the observed spontaneous potentials were the same as the stimulated ones and not potentials associated with other unidentified conduction systems, electrical stimuli were applied, in the usual manner, immediately after a spontaneous potential was observed. When this was done after a spontaneous through-conducted potential had been recorded, a single through-conducted potential was recorded from both electrodes. The delay between the stimulus artifact and the recording of the potentials on each trace matched that which would be expected for a stimulated through-conducted potential traveling through the pathways involved. However, the stimulated potentials invariably included muscle action potentials and were therefore larger than those normally evoked by a single stimulus. The presence of the muscle action potential on the stimulated potential indicated that the spontaneous potential must have had the same effect on the muscles of a polyp as a stimulated potential, and therefore proved that both types of through-conducted potentials were identical. The appearance of the spontaneous potentials in the apparent absence of stimulation may have been a consequence of mechanical stress caused by the presence of the electrodes. They may also be a feature of undisturbed colonies, but no evidence was available to support this possibility.

Similar experiments were done to ascertain whether the isolated potentials were the same as the through-conducted ones. These experiments were preceded by a series of controls. These controls consisted of a pair of electrical stimuli applied to the colony, in the usual manner, at the beginning of an experiment, and at random intervals during it. Normally, the potentials evoked by stimulation of the

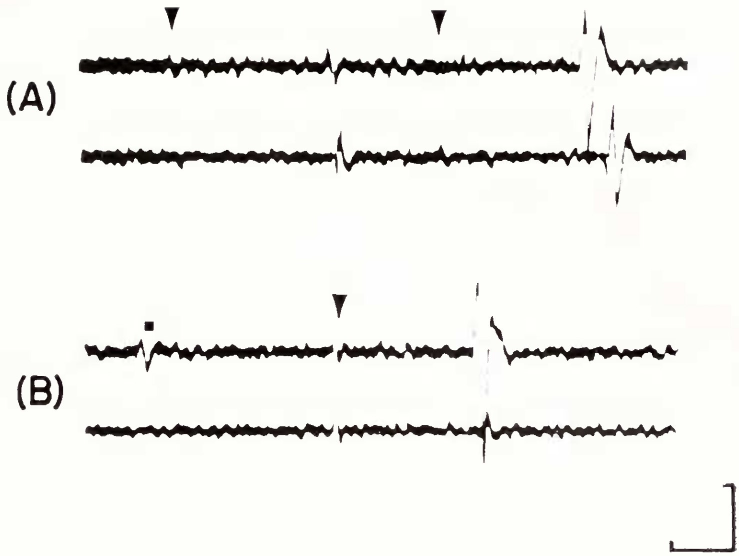

FIGURE 3. (A) Electrical activity recorded as in Figure 2A. These records served as a control for later experiments illustrated in Figure 3B. (B) Effect of electrical stimulation of *Tubipora* after an isolated potential (marked with a dot on the upper trace) has been recorded. Note that the amplitude of the potentials evoked by the electrical stimuli are no longer equivalent. (Ordinate and abscissa are as for Figure 2.)

colonial conduction system were equivalent. That is, after a single stimulus a single, small potential was recorded from polyps all over the colony; while a second stimulus evoked potentials which contained both muscle action potentials and the small impulse triggered by the first stimulus (Fig. 3A). Invariably, the muscle action potentials are of equivalent sizes. When a single stimulus was applied after an isolated potential had been observed, two through-conducted potentials were recorded (Fig. 3B). Unlike the potentials recorded after the control stimuli, these potentials were not of an equivalent size. In Figure 3B, the evoked potential on the lower trace consists only of the small potential typical of that normally evoked by the first stimulus of a series. The evoked potential on the trace containing the isolated potential (upper trace) contains a muscle action potential. In other experiments, both evoked potentials occasionally contained a muscle action component. However, in these instances, the muscle action potential recorded from the same polyp as the isolated potential was always larger. This evidence indicates that a single, isolated potential must have had the same effect on the muscles of a polyp as a single through-conducted potential; it facilitated those muscles so that a second potential, whether through-conducted or not, could activate those muscles and produce a twitch of the polyp.

The effect of magnesium ions on the colonial conduction system was determined by replacing the sea water in the preparation bath with a 50% solution of isosmotic $MgCl_2$ in sea water. Recordings were made during the perfusion process, and the

colony stimulated once every two minutes with a train of three or four stimuli. Normal facilitating potentials were recorded after 55 minutes of immersion in the magnesium sea water.

Discussion

Polyp retraction is the only observable colonial behavior of *Tubipora musica*. While it is possible that others do exist, they have not been revealed by either this study or that of Horridge (1957). The conduction system responsible for control of this behavior is through-conducting over the entire colony. Potentials recorded from this conduction system are composed of two components: a small potential that can be recorded from the conduction system itself; and a second, larger, facilitating potential that has been interpreted as a muscle action potential. It is probable that the muscle action potentials originate in the muscles responsible for polyp retraction. Because of the relationship between the triggering potential from the colonial conduction system and the muscle action potentials, the recordings from *Tubipora* resemble many of the classic facilitating neuromuscular potentials reported by previous investigators (Josephson, 1966; Robson and Josephson, 1969; Pickens, 1974).

Perfusion of the preparation bath with magnesium sea water had little effect on both the propagation of potentials through the colony and the appearance of the facilitating potentials recorded from the polyps. It is generally accepted that whereas excess Mg^{++} ions interfere with nervous and neuromuscular processes, they have little effect on epithelial conduction systems. This conclusion has been derived from the effects of solutions similar to those used here, on siphonophores (Mackie, 1965) and hydromedusae (Mackie and Passano, 1968) where both epithelial and neural conduction systems have been identified by histological, physiological and behavioral criteria. The effect of magnesium ions alone is far from sufficient evidence for claiming that a conduction system is neuroid. However, the degree of insensitivity to magnesium displayed by *Tubipora* is surprising, particularly when considered in terms of the effect of magnesium on other anthozoans. Excess Mg^{++} rapidly blocks activity in all three identified conduction systems in sea anemones (Robson and Josephson, 1969; McFarlane, 1969), in the two colonial conduction systems in the pennatulid *Renilla köllikeri* (Anderson and Case, 1975) and completely anesthetizes colonies of the madreporarian hard coral *Goniopora lobata* (Anderson, in preparation). Certain of these conduction systems, the SS1 and SS2 in anemones (McFarlane, 1969; Shelton, 1975b) and one of the colonial conduction systems in pennatulids (Shelton, 1975c) may be epithelial. The action of magnesium in all these cases is rapid, in complete contrast to the results found for *Tubipora*. It is conceivable, however, that the insensitivity displayed by *Tubipora* may be a result of inaccessibility of the nerves or some other factors. Consequently, it is too early to designate a morphological basis to the colonial conduction system responsible for polyp retraction. In the meantime, it will be referred to simply as the colonial conduction system.

All potentials recorded in this study have been shown to have originated in a single conduction system, the colonial conduction system. The absence of multiple

conduction systems may be somewhat atypical of anthozoans. In sea anemones, there are, in addition to the through-conducting nerve net, two "slow conduction systems" (McFarlane, 1969). In some pennatulids, there are two colonial conduction systems (Shelton, 1975c; Anderson and Case, 1975), a through-conducting nerve net and a second system which has been equated with the "slow systems" in anemones (Shelton, 1975c). There is also circumstantial evidence of a "slow conduction system" in certain hard corals (Shelton, 1975d). While it is conceivable that improvements in recording techniques may reveal potentials originating in other conduction systems, the apparent absence of multiple conduction systems in *Tubipora* may be a reflection of a limited repertoire of colonial behavior.

A mechanism by which the autonomy of individual polyps can be maintained emerges from these results. Isolated potentials are restricted to individual polyps where they appear to originate in a conduction system responsible for controlling the behavior of the polyp. This is evidenced by the fact that mechanical stimulation of a polyp evokes an isolated potential. Similar stimuli can also provoke withdrawal of a polyp through a series of stages very reminiscent of the same process in sea anemones (Pantin, 1935 a,b,c,d). Because the isolated potentials are identical to through-conducted potentials, both in their shape and their effect on the muscles of a polyp, it would appear that the potentials recorded during colonial activity are in fact isolated potentials that are evoked sequentially in all the polyps by the wave of colonial activity that spreads away from the stimulating site. It is not possible to say at this stage, whether the conduction system in the polyps is an integral part of the colonial conduction system or a second conduction system which is triggered once by each colonially conducted potential. It is apparent, however, that the connection between the conduction system in the colony and that in the polyp is not through-conducting in both directions. Through-conducted potentials can enter polyps easily. This is illustrated by the fact that each stimulus applied to the colonial conduction system evokes a potential which can be recorded from polyps all over the colony. However, potentials which originate in a polyp, isolated potentials, rarely pass into the colonial conduction system and only then in instances when a polyp has been strongly stimulated. This would indicate that there is some kind of polarization of the connection between the conduction system in individual polyps and that operating through the colony as a whole. Since the morphological basis of the conduction system in *Tubipora* is unclear, speculation as to the means by which the polarization could be brought about would be pointless. Polarization of a similar nature has been described in the colonial hydroid *Hydractinia* (Stokes, 1974) where stimulation of the basal mat can evoke a propagated response involving lashing of dactylozooids. Direct stimulation of a dactylozooid does not, however, affect other dactylozooids in the colony.

The arrangement of conduction systems in *Tubipora* is similar to that already described for *Renilla* (Anderson and Case, 1975) with the exception that there is apparently only one colonial conduction system in *Tubipora.* The colonial conduction system responsible for controlling polyp retraction is through-conducting in both cases, and polyp withdrawal may involve activation of a second conduction system restricted to individual polyps. However, the arrangement in *Tubipora* differs in that each colonially conducted potential affects the muscles of the polyps, with

facilitating muscle action potentials being recorded after every stimulus except the first of a series. In *Renilla* several colonially conducted Nerve Net pulses are required before a burst of Zooid Nerve Net pulses is produced and withdrawal occurs. Because *Tubipora* polyps respond to every colonial potential, flexibility inherent in the interaction between the colonial Nerve Net and the Zooid Nerve Net in *Renilla* polyps is lost. Despite this, *Tubipora* achieves the same end of having a mechanism whereby the activities of any one polyp can be kept separate from others in the colony. However, this separation is not so complete that a colonial response cannot occur.

I am very grateful to Dr. J. F. Case for allowing me to participate on the expedition and for his comments on the manuscript. My thanks also to Dr. R. K. Josephson for helpful discussions during the course of the experiments and his valuable comments on the manuscript. This paper is part of a thesis to be presented to the Department of Biological Sciences, University of California, Santa Barbara in partial fulfillment of the requirements for the Ph.D.

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Summary

1. Through-conducted electrical activity can be recorded from colonies of *Tubipora musica* after mechanical and electrical stimulation.

2. The recorded potentials, conducted with a maximum velocity of 18 cm/sec, show distinct facilitation of a component interpreted as a muscle action potential. The colonially conducted potentials responsible for muscle activation in the polyps appear on the records as small (5 μV) potentials that precede the muscle action potentials.

3. The propagation and form of all recorded electrical activity is unaltered after 55 minutes submersion of *Tubipora* in a solution containing high magnesium.

4. Commonly, potentials similar to those associated with colonial activity can be recorded from only one polyp. These are interpreted as being the result of some form of polarization between the conduction system in the polyp and that in the colony which allows individual polyps to function independently of the remainder in the colony.

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